

**Thesis/  
Reports  
Biesinger,  
Z.**

**Direct and Indirect Parametrization  
of a Localized Model for the  
Mountain Pine Beetle --  
Lodgepole Pine System**

*Final Report  
RMRS 98566 RJVA*

# Direct and Indirect Parametrization of a Localized Model for the Mountain Pine Beetle – Lodgepole Pine System

Zy Biesinger\* and James Powell†

Department of Mathematics and Statistics

Utah State University

Logan UT 84322-3900

Barbara Bentz and Jesse Logan‡

USDA Forest Service Rocky Mountain Research Station

Logan Forestry Sciences Laboratory

and Department of Forest Resources

Utah State University

January 4, 1999

## Abstract

The dynamic interaction between mountain pine beetles (MPB) and hosts (generally lodgepole pine) is reviewed briefly. The 'local' projection of a partial differential equation model describing this interaction is employed in parameter estimation. Methods and assumptions for estimating non-fitted parameter values are given. Assigning values to non-fitted parameters, direct and indirect parametrization techniques are employed to estimate remaining parameter values. The indirect method is quickly and easily applied to many data sets but requires some assumptions and model simplifications. The direct method requires fewer assumptions but is computationally intensive. The results of these two techniques are compared and evaluated.

## 1 Introduction

The spatial redistribution of organisms in an ecosystem is often a complex process. Many ecosystems exhibit spatial complexity on a broad range of scales, driven by the physical environment and biotic interactions [46]. As different species aggregate and disperse in spatially complex ways, even an initially uniform environment can soon evolve spatial heterogeneity. There are a variety of factors that drive the spatial dynamics of a population, including

---

\*Corresponding author, email at zy@biology.usu.edu

†Dr. Powell and Mr. Biesinger were supported by NSF grant DMS-9505327, an REU supplement and the USDA Forest Service Mountain Pine Beetle Project

‡Drs. Bentz, Logan and Powell were supported by NSF grant DMS-9505327 and the Utah Mineral Lease Replacement Program

defense against predators, success as predators, and reproductive success. Also, spatial complexity can arise from dispersal and aggregation. When an organism is itself responsible for chemical, auditory, visual or other cues which lead to aggregation, nonlinear feedback can occur, creating self-organized groups of individuals (self-focusing). Self-dissipation also plays an important role in many ecosystems' dynamics. Interaction between self-focusing and self-dissipating forces leads to complex spatial reorganization of populations of organisms.

Spatial dynamics typically play a central role in the community dynamics of highly mobile insects [57], such as mountain pine beetle (MPB, *Dendroctonus ponderosae* Hopkins) [38]. The MPB/pine tree host (for example, spp. *Pinus contorta*) system has long been the subject of research because of the economic and ecological impact. As an aggressive bark beetle (one that kills its host), eruptions of this species are impressive events resulting in intensive and extensive outbreaks. It is also becoming recognized that disturbances, such as insect outbreaks, may be central to maintaining the structure, function and health of western forests [52, 48, 25, 47].

One method to help understand this dual role of bark beetles as an economic competitor and as a co-evolved component of the ecosystem is the development and analysis of quantitative models [6, 8, 39, 40, 4, 11, 7, 51, 31, 56, 57]. These spatially independent models have achieved some success, but fail to capture the full sequence of events necessary for successful population establishment and expansion. Aggregation on and dispersal from a host are of such overriding importance to MPB ecology that including spatial dynamics in model representations is essential for ecological credibility. Powell *et al.* [35] built upon past models to develop a large-scale (forest-sized) reaction-diffusion partial differential equation (PDE) model of the spatial interaction between MPB and its host trees. To facilitate experimentation and parametrization, a 'local' projection of the PDE model into a single system of ordinary differential equations (ODEs), has been developed [36]. The purpose of the current paper is to use field data to estimate parameters for the model. Validation will be presented in future manuscripts.

## 1.1 System Description and Behavior

During a relatively short flight period during late summer, adult MPB fly in search of suitable host trees into which females deposit eggs. The following year, with warming spring temperatures, juvenile MPB move horizontally through the phloem tissue, feeding on the energy rich products of photosynthesis. Pine tree hosts do not passively submit to MPB attacks; they have evolved physiological mechanisms to resist beetle attacks [53, 54, 44, 28, 42]. When a beetle bores into a tree, the tree responds by flooding the gallery with resin which serves as a chemical and physical barrier to the beetle.

Because a tree can repel many attacks before being overcome, beetles must synchronize their emergence and coordinate their attacks on a specific host tree quickly enough to deplete the resin reserves [1]. Only those trees with a rapid and sustained reaction are likely to survive an MPB mass attack [7, 42]. To coordinate attacks, MPB have evolved a chemical communication system [29, 30, 18] based on diffusible aggregation [14, 10, 26, 17, 16] and anti-aggregation [19, 21, 49, 50] pheromones and kairomones [15, 27, 47, 45].

Once an attack has been initiated, attacking female MPB convert  $\alpha$ -pinene, a major constituent of the resin of *Pinus* spp. into *trans*-verbenol [19]. As the number of attacking

MPB increases, higher concentrations of *trans*-verbenol attract higher proportions of male MPB [45]. Males produce *exo*-brevicomin, which at low concentrations attracts primarily females [14].

This nonlinear self-focusing has the potential to attract large numbers of MPB. Overcolonization is avoided via the anti-aggregation arm of the pheromone communication system. In addition to aggregants, attacking males and females release a suite of compounds resulting in a close-range redirection of responding beetles to nearby trees [10, 26, 16, 3]. This chemical communication system allows beetle populations to survive from year to year at endemic levels, killing only weakened trees. As population numbers grow, more vigorous and more nutritional trees can be overcome. When populations grow large enough, an outbreak results, in which thousands of acres of pine trees are killed.

## 1.2 Global Model

The mass dispersal behavior of the MPB/host tree system is described by a model [35, 36, 37, 33, 32] using density variables depending on spatial location,  $x, y$ , and time,  $t$ . The state variables are:

- $Q(x, y, t)$  – population of MPB attacking susceptible trees.
- $H(x, y, t)$  – number of entrance holes bored by attacking MPB.
- $S(x, y, t)$  – resin outflow.
- $R(x, y, t)$  – resin capacity of initially uninfested trees.
- $P(x, y, t)$  – population of MPB dispersing from previous year's infested trees.
- $A(x, y, t)$  – concentration of pheromones.

The model equations are:

$$\dot{Q} = -\omega_2 Q + r_1 \frac{R}{R_0} P - \beta S \frac{Q}{H}, \quad (1)$$

$$\dot{H} = r_1 \frac{R}{R_0} P - r_4 r_3 H R, \quad (2)$$

$$S = r_3 H R,$$

$$\dot{R} = [r_2(R_0 - R) - r_3 H] R, \quad (3)$$

$$\frac{\partial}{\partial t} P = -\nabla \cdot \{[\nu \nabla f(A)] P - \mu \nabla P\} - \omega_1 P - r_1 \frac{R}{R_0} P + \gamma \quad (4)$$

where

$$f(A) = A_3 A_0 \left\{ (A_3 + 1) \ln \left[ 1 + \frac{A}{A_3 A_0} \right] - \frac{A}{A_0} \right\},$$

and

$$\frac{\partial}{\partial t} A = b_1 \nabla^2 A + a_1 Q - \delta_1 A. \quad (5)$$

The population of beetles attempting to nest is described by (1), while the number of open entrance holes bored by attacking beetles is modeled by (2). The amount of resin outflow,  $S$ , enters the system as the loss term of equation (2). The local resin capacity and the amount of resin outflow with time are described by equation (3). Equation (4) describes changes in flying MPB density and includes a term for the spatio-temporal evolution of  $P$  depending upon chemical concentrations,  $A$ . Finally, equation (5) models pheromone concentrations as they vary through time and space. Equations (1 - 5) are a complete spatio-temporal description of the dependent variables controlling the behavior of MPB/pine relationship.

### 1.3 Localization of the Global Model

The global model, describing dynamics on a forest-sized scale, has proven to be too complicated for ecological use, because variables describing an entire forest are spatially and temporally extended. Localizing the global model will convert variables from densities to numbers at a point. It is this type of number that field studies generate. This allows the use of observational data to approximate parameter values which best fit the local model to observed system dynamics. To localize the model we investigate the consequences of the global model at a single location (for example, an individual host) [35]. Local model variables depend only on time,  $t$ :

- $q(t)$  – population of (alive) nesting MPB in a tree.
- $h(t)$  – number of open attack holes in a tree.
- $r(t)$  – resin capacity of a tree.
- $a(t)$  – number of pheromone molecules at a point.
- $w_a(t)$  – characteristic area occupied by the pheromone plume from a single host.
- $I(t)$  – local population of dispersing MPB.

With these variables we construct the local model following the localization method described in [35, 36] equations.

$$\dot{q} = r_1 \frac{r}{r_0} I - \beta \frac{r_3}{w} q r, \quad (6)$$

$$\dot{h} = r_1 \frac{r}{r_0} I - \frac{r_3}{w} r_4 h r, \quad (7)$$

$$\dot{r} = r \left[ \frac{r_2}{w} (r_0 - r) - \frac{r_3}{w} h \right], \quad (8)$$

$$\dot{a} = a_1 q - \delta_1 a, \quad (9)$$

$$\dot{w}_a = 4b_1 + a_1 q \frac{w - w_a}{a}, \quad (10)$$

and

$$I = \frac{\pi \gamma r_e^2}{r_1 + \omega_1} \exp \left[ \frac{\nu}{\mu} f(q) \right] \quad (11)$$

where

$$f(q) = A_3 A_0 \left\{ (A_3 + 1) \ln \left[ 1 + \frac{2a_1 q}{A_3 A_0 (4b_1 + w\delta_1)} \right] - \frac{2a_1 q}{A_0 (4b_1 + w\delta_1)} \right\}.$$

A list of parameter definitions is presented in Table 1.

## 2 Methods

### 2.1 Experimental Design and Data Collection

During the summer of 1995, three sites, at least a quarter of a mile apart, were selected in a lodgepole pine stand in the Gold Creek drainage of the Sawtooth National Recreation Area (SNRA), Idaho. One MPB pheromone bait was attached to a single focus tree at each site and removed after twenty-four hours. Based on emergence data from a nearby experiment [2] beetle flight in the area had just begun. For twelve days MPB attacks on the basal 2.1 metres of individual trees were counted twice a day on all host trees within ten metres of the focus tree. By monitoring MPB attacks on individual trees we were able to create a time series of the landing and attack of recently emerged beetles [3] (Figures 1 and 2). Due to lack of attacked trees in two of the plots, only results from successfully attacked trees in one plot are reported.

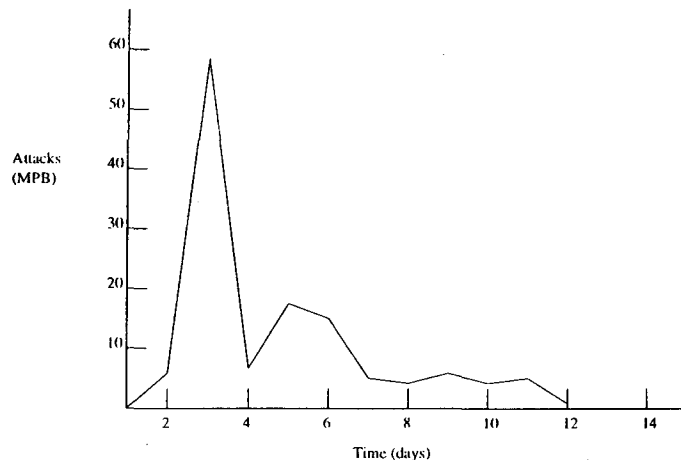


Figure 1: Example of MPB attack series on a single host which exhibits expected system dynamics, a rapid increase in the number of attacks followed by a sharp drop. This figure shows MPB attacks on the basal 2.1 metres of tree 3 from the 1995 SNRA data.

Two similar sites were established in 1996 near St. Charles, Idaho. In 1997, five plots were monitored, two new sites near St. Charles and three in the Williams Creek drainage in the SNRA. The focus tree of each plot was artificially baited to initiate mass attacks in the plots

Parameter Definitions and Units		
Parameter	Definition	Units
$A_0$	Critical concentration at which pheromones become repulsive	$\mu\text{g}/\text{ha}^{-1}$
$A_3$	Saturation parameter for pheromones	—
$a_1$	Rate of pheromone production by nesting beetles	$\mu\text{g} \cdot \text{fh}^{-1} \cdot \text{HMPB}^{-1}$
$\beta$	Mortality rate of beetles due to resin outflow	$\text{ha}^{-1} \cdot R_0^{-1}$
$b_1$	Rate of pheromone diffusion	$\text{ha}/\text{fh}$
$\delta_1$	Loss rate of pheromones	$\text{fh}^{-1}$
$\ell$	Distance from the focus tree	$\text{ha}^{\frac{1}{2}}$
$\mu$	Diffusivity of flying beetles due to random movement	$\text{ha}/\text{fh}$
$\nu$	Strength of directed MPB motion due to pheromone gradients	$\text{ha}^2 \cdot \mu\text{g}^{-1} \cdot \text{fh}^{-1}$
$r_0$	Rest resin capacity of a healthy tree	$\text{ha} \cdot R_0$
$r_1$	Rate of random landing and conversion from flying to nesting beetles	$\text{fh}^{-1}$
$r_2$	Rate of resin replenishment	$\text{fh}^{-1} \cdot R_0^{-1}$
$r_3$	Rate of resin outflow through holes bored by beetles	$\text{ha}/\text{fh}$
$r_4$	Rate of resin crystallization (tree recovery)	$\text{ha}^{-1} \cdot R_0^{-1}$
$r_e$	Conversion factor for transforming the density of flying MPB into the number of MPB attacks; or ‘radius of engagement’	$\text{ha}^{\frac{1}{2}}$
$\sigma$	Parameter describing the openness of a stand of trees	—
$\omega_1$	Death rate of airborne beetles	$\text{fh}^{-1}$
$\omega_2$	Death rate of nesting beetles	$\text{fh}^{-1}$
$w$	Parameter representing the characteristic size of a tree	$\text{ha}$
$\gamma(t)$	Emergence rate of flying beetles, temporally dependent	$\text{HMPB} \cdot \text{ha}^{-1} \cdot \text{fh}^{-1}$

Table 1: List of parameters appearing in the global PDE and local ODE models for MPB redistribution. Density units are presented with respect to hectares (ha), pheromone amounts in micrograms ( $\mu\text{g} = 10^{-6}\text{g}$ ), and numbers of MPB are counted in hundreds (HMPB). The basic unit of time is the flight hour (fh), of which there are approximately five per day.



and the baits were removed once attacks had begun. All host trees within a radial distance of 14 metres were monitored twice a day. MPB attacks were measured between 0.7 and 1.75 metres from the base of each tree. Relative to temperatures during the 1995 experiments, temperatures fluctuated widely during the 1996 and 1997 experiments. Figure 2 depicts an attack series that does not conform to expected system behavior. The fluctuations in the attack series were likely influenced by corresponding fluctuations in temperature.

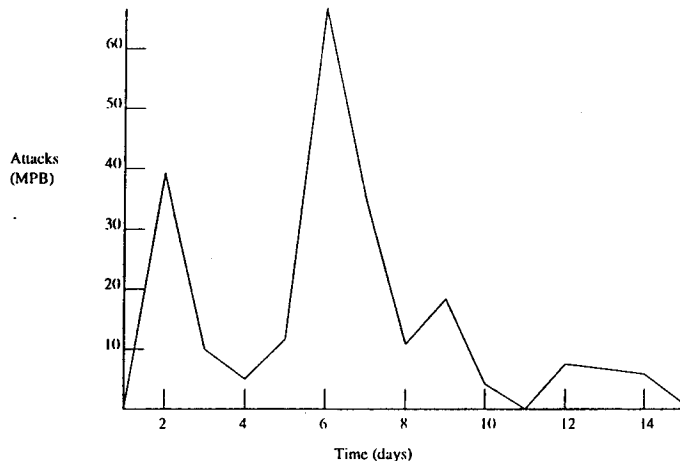


Figure 2: Example of MPB attack series on a single host which does not exhibit expected system dynamics; showing multiple large peaks in attack numbers. This figure represents MPB attacks on 1.05 metres of the bole of tree 2 in plot 2 from the 1997 St. Charles data.

To gather data for the purpose of validation, several weeks after beetle flight had ceased in the 1997 St. Charles area we returned to the sites in order to estimate the final number of beetles nesting in successfully attacked trees. We took counts of all attacks in 0.1225 m<sup>2</sup> on the north and south aspect of each tree at heights of 0, 1.4, 2.8, 4.2 and 5.6 metres. Also, we estimated the total height of attack on each tree. In parametrizing the model we assumed the maximum attack height to be 7.3 metres [39, 20], although this number varied depending on the size of a particular tree. Using a general maximum attack height to parametrize the model we hope to obtain parameter values generally applicable to all trees. Then using observed maximum attack heights we will be able to evaluate how well the generalized parameters capture true, variable system dynamics.

## 2.2 Local Parameter Values

The parameters to be estimated fall in two categories: ‘behavioral’ parameters ( $\nu, \mu, A_0$ ) controlling MPB dispersal and ‘local’ parameters for the MPB attack/host response interaction, which can, in principle be measured purely on a tree-by-tree basis. Here our focus is on the ‘behavioral’ parameters; for the local parameters we will use estimates based on information from the literature and personal experience. A survey of these estimates is presented as an appendix and closely follows results presented in [35, 36, 22]. In addition, the behavioral parameter for random dispersal,  $\mu$ , has been estimated by Turchin and Theony [57] for southern pine beetle, (*Dendroctonus frontalis*), which estimate we use here for MPB. Parameter values thus determined are presented in Table 2.



Non-fitted Parameter Values			
Parameter	Value	Parameter	Value
$A_3$	1	$a_1$	$2 \mu\text{g} \cdot \text{fh}^{-1} \cdot \text{HMPB}^{-1}$
$b_1$	$\frac{0.324}{\sigma} \text{ ha/fh}$	$\beta$	$8 R_0^{-1}$
$\delta_1$	$360\sigma \text{ fh}^{-1}$	$\mu$	$1.0 \text{ ha/fh}$
$r_0$	$1 \text{ ha } R_0$	$r_1$	$0.16 \text{ fh}^{-1}$
$r_2/w$	$0.1 \text{ fh}^{-1} \cdot R_0^{-1}$	$r_3/w$	$0.05 \text{ fh}^{-1}$
$r_4$	$2 R_0^{-1}$	$r_e$	$0.02 \text{ ha}^{\frac{1}{2}}$
$\sigma$	$0 - 1$	$w$	$0.003 \text{ ha}$

Table 2: List of parameter values estimated using literature and knowledge of the systems involved. Units involving resin are measured relative to  $R_0$ . Other units are :  $\mu\text{g}$  ( $10^{-6}$  grams), ha ( $10^4$  square metres = hectares), fh (flight hours  $\sim 5$  fh/day).

The remaining two behavioral parameters,  $A_0$  and  $\nu$ , are difficult to estimate from previous information and data.  $A_0$  describes the critical concentration of pheromone which results in beetles redirecting their attack to a new tree, and  $\nu$  describes the strength of a directed MPB flight caused by pheromone gradients. By assigning values to other model parameters, we can approximate values for  $A_0$  and  $\nu$  by fitting model predictions to field data. Also,  $\gamma(t)$ , the emergence rate, will be left free since it potentially varies in magnitude and shape from site to site. Due to this potentially large variation, estimates of  $\gamma(t)$  are not generally applicable and will not be reported. Two separate fitting methods, each with its own advantages and disadvantages will be used to estimate these parameters using the field collected data.

## 2.3 Model Parametrization

To estimate remaining parameters in the local model we employ two methods. Initially we use an indirect fitting technique which can be quickly and easily applied to MPB attack series of many trees. This technique requires several simplifications of the local model and assumptions about system conditions which increase error propagation, but is a computationally simple way to obtain estimates for values of  $A_0$  and  $\nu$ . To check the effectiveness and robustness of the indirect method, we apply a second, computationally intensive method to a subset of the same trees' attack series. Although the direct fitting technique requires much more time than the indirect method, it has the advantage of requiring fewer assumptions.

### 2.3.1 Indirect Fitting Method

The indirect fitting method is based on the assumption that the number of new MPB attacks on a tree largely depends on the number of beetles already nesting in that tree. Making the assumption that the field collected data reflects the rate of attack by MPB on individual trees, the number of new attacks,  $A_n$ , corresponds to the infestation term appearing in (6)

and (7):

$$r_1 \frac{r}{r_0} I.$$

We can use this assumption to estimate  $A_0$  and  $\nu$ , which are embedded in the infestation function,  $I$  (11),

$$I = \frac{\pi \gamma r_e^2}{r_1 + \omega_1} \exp \left[ \frac{\nu}{\mu} \left\{ A_3 A_0 \left( (A_3 + 1) \ln \left[ 1 + \frac{2a_1 q}{A_3 A_0 (4b_1 + w\delta_1)} \right] - \frac{2a_1 q}{A_0 (4b_1 + w\delta_1)} \right) \right\} \right].$$

By replacing the infestation term in (6) and (7) with the field data,  $A_n$ , we use a stepwise approximation of the local model and calculate the number of nesting beetles that is required for the model to predict the number of new attacks actually observed. This will generate ordered pairs consisting of the number of nesting beetles required to attract an observed number of new attacks (the dependent variable) and the number of new attacks (the independent, observed variable),  $\{q_n, A_n\}$ . Since the number of infesting beetles predicted by the infestation term,  $r_1 \frac{r}{r_0} I$ , depends directly on the number of nesting beetles,  $q$ , we can use the calculated number of nesting beetles,  $q_n$ , to obtain predictions from the infestation term of how many new attacks to expect at the next time step. This generates a second set of ordered pairs,  $\{q_n, r_1 \frac{r}{r_0} I(q_n)\}$ , consisting of the number of nesting beetles (the calculated, independent variable) and the number of new attacks predicted by the infestation term (the dependent variable.) Using a non-linear least-squares fitting technique, we can then estimate  $A_0$  and  $\nu$ .

Leaving  $A_0$  and  $\nu$  free and assigning values to the other parameters leaves only the function describing the emergence rate of adult beetles,  $\gamma(t)$ , to be defined. In principle  $\gamma$  is a directly-measurable function, the density of MPB emerging in the ‘background’ of the plot. In practice it can vary extremely with temperature, shifts of wind, and spatio-temporal fluctuations in the emergence of MPB from host trees in the vicinity. Collecting this data was well beyond the scope of our study. Instead, from the local perspective  $\gamma(t)$  is just the temporal attack ‘forcing’ perceived within a plot, and therefore a step-wise approximation to  $\gamma(t) \doteq \gamma(t_n) = \gamma_n$  is

$$\gamma_n = \tau \sum_{j=1}^{\text{all trees}} (\text{attacks on tree } j)_n,$$

where  $n$  is a time index and  $\tau$  is a scaling factor between attacks in a plot and beetle activity in the area (which, for convenience, encompasses  $\frac{\pi}{r_1 + \omega_1}$  in (11).) When solving model equations we replace  $\gamma(t)$  with the scaled interpolated function,  $\gamma_n$ .

The ordered pairs will be as follows, where  $A_n$  represents new attacks on a tree at each time step,  $n$ , extrapolated from attacks observed on a portion of the bole. We assume an average attack height of 7.3 metres [39, 20].

$$\{q_n, A_n\} \text{ vs. } \left\{ q_n, r_1 \frac{r_n}{r_0} I(q_n) \right\}.$$

Since the infestation function is exponential and logarithmic (11) it is very sensitive to changes in the value of  $q$ . We manipulate the correspondance of

$$A_n \sim r_1 \frac{r_n}{r_0} I(q_n)$$

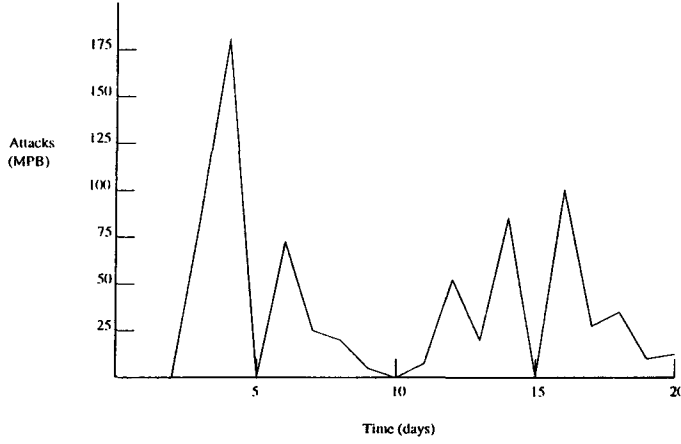


Figure 3: MPB attacks on 1.05 metres of tree boles in the entire 1997 SNRA plot 3, during the summer flight period. This data can be used to provide the shape of the function describing background emergence,  $\gamma$ , including variations of temperature and emergence non-parametrically.

and apply a logarithmic transform to make the infestation function less sensitive. Thus, the problem becomes to choose  $\nu$ ,  $A_0$ , and  $\tau$  to maximixe the correspondence between

$$\left\{ q_n, \ln \left[ \frac{A_n r_0}{r_1 r_n} \right] \right\} \text{ and } \{ q_n, \ln[I(q_n)] \}.$$

To create these ordered pairs and use the observed data in the parametrization of the local model we must first construct a stepwise model that will allow us to back-calculate the number of beetles nesting in a tree at the beginning of any given time step based upon the number of new attacks observed during the that time step. This requires some simplifying assumptions about the physical characteristics of the system.

From (8), assuming that  $r$  does not equal zero (the case where the tree is dead) and that, on our time scale, the change in tree vigor,  $\dot{r}$ , is small, we can estimate  $r$  to be

$$r = r_0 - \frac{r_3}{r_2} h.$$

In (7), taking the rate of resin crystallization,  $r_4$ , to be slow on the time scale of beetle activity gives

$$\dot{h} = r_1 \frac{r}{r_0} I.$$

The right-hand side of this equation is the part of the model that corresponds to the observational data, the number of attacks per time on a particular tree. We replace this part of the model with our observational values and define the following stepwise terms based on the preceding assumptions:

$$\begin{aligned}
h_n &= \text{sum of attacks observed from time 1 to } n \\
&= \sum_{i=1}^n A_i,
\end{aligned}$$

$$\begin{aligned}
r_n &= \text{initial resin capacity of a tree - resin loss due to attack holes} \\
&= r_0 - \frac{r_3}{r_2} h_n,
\end{aligned}$$

$$\begin{aligned}
\dot{q}_n &= \text{rate of new attacks - rate at which beetles are repelled by tree defenses} \\
&= \frac{A_n}{\Delta t} - \beta r_3 q_n r_n.
\end{aligned}$$

An example of  $h_n$  for one tree is seen in Figure 4. In the equation for  $\dot{q}_n$  we can assume that  $A_n$  and  $r_n$  are constant at a given time step. For  $\Delta t$  we can use one time step,  $n - 1$  to  $n$ , which corresponds to an initial condition for  $q_n$  given by  $q_{n-1}$ . Solving the above differential equation for  $q_n$ , assuming  $r = \text{constant} = r_n$  and constant forcing,  $A_n$ , is

$$q_n = \frac{A_n}{\beta r_3 r_n \Delta t} [1 - \exp(-\beta r_3 r_n \Delta t)] + q_{n-1} \exp(-\beta r_3 r_n \Delta t).$$

With this stepwise model we can use the number of attack holes currently in a tree and estimate the number of beetles nesting at the previous time step. This will generate the first of the ordered pairs. The estimated number of nesting beetles can then be used in the infestation function to create the second set of ordered pairs.

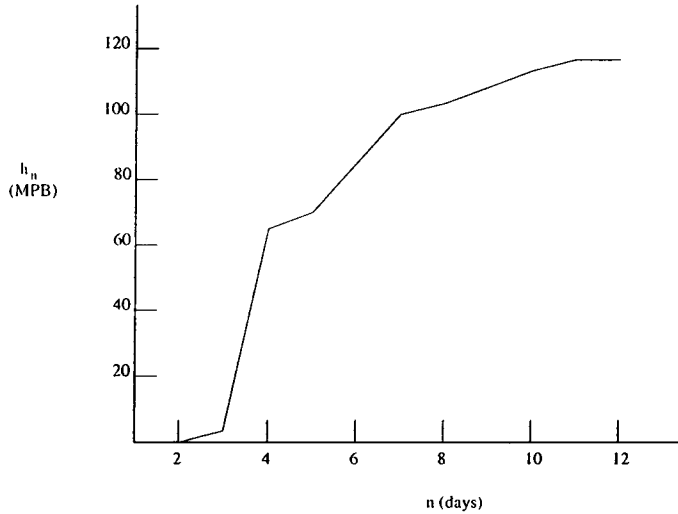


Figure 4: Representation of all MPB attacks,  $h_n$ , on the basal 2.1 metres of a single host up to day 12. This figure depicts the summed attacks of tree 3 from the 1995 SNRA data.

Our goal is to fit the model-predicted ordered pairs,  $\{q_n, \ln(I(q_n))\}$ , to the data derived pairs,  $\{q_n, \ln(\frac{A_n r_0}{r_1 r_n})\}$ , by choosing values for  $A_0$  and  $\nu$ , which are embedded in  $I$  (Figure 5). We employ a least-squares regression method to fit model predictions to observational data. Specifically, we use *Mathematica*'s `NonlinearRegress` routine [24] which performs their `LevenbergMarquardt` method, gradually shifting the search from steepest descent to quadratic minimization.

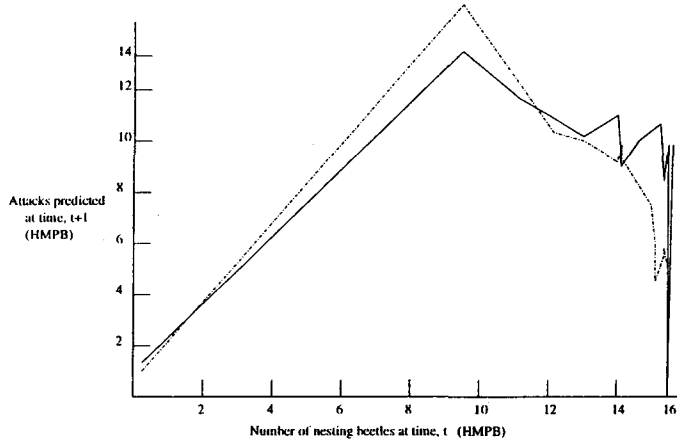


Figure 5: Comparison of manipulated experimental data ( $\{q_n, \ln(\frac{A_n r_0}{r_1 r_n})\}$ , solid line) and model predictions ( $\{q_n, \ln(I(q_n))\}$ , dashed line) of MPB attacks on an entire tree using the indirect fitting procedure and the attack series of tree 5 from the 1997 St. Charles plot 1 data.

### 2.3.2 Direct Fitting Method

The 'Direct' fitting approach is to actually guess parameters  $A_0$ ,  $\nu$ , and  $\tau$ , solve equations (6-11) numerically, and then evaluate the error by summing the absolute deviation between model predictions for  $r_1 \frac{r}{r_0} I$  and  $A_n$ . Parameters which minimize the absolute deviation are deemed 'best' fits. The direct algorithm is summarized in pseudo-code below:

Assign all parameter values except  $A_0$ ,  $\nu$  and  $\gamma$

Define  $\gamma_n = \tau$  (total daily attacks) <sub>$n$</sub>

Define  $I(q(n), \gamma_n) = \gamma_n r_e^2 \exp\left[\frac{\nu}{\mu} f\left(\frac{a_1 q(n)}{4b_1 + w\delta_1}\right)\right]$

Assign starting value of  $A_0$

Start Loop 1

    Assign starting value of  $\nu$

    Start Loop 2

        Assign starting value of  $\tau$

        Start Loop 3

            Solve model equations

            Calculate absolute error between model predictions and data,

$$\text{error} = \sum_{n=1}^{\text{all days}} \left| r_1 \frac{r(n)}{r_0} I(q(n), \gamma_n) - A_n \right|$$

        Store current values  $\{\tau, \text{error}\}$

        Increment  $\tau$

    End Loop 3

    Choose smallest error measurement with the corresponding  $\tau$  and store them with current values of  $A_0$  and  $\nu$ :  $\{A_0, \nu, \tau, \text{minimum error}\}$

Increment  $\nu$   
 End Loop 2  
 Increment  $A_0$   
 End Loop 1  
 Choose values of  $A_0$  and  $\nu$  corresponding to the smallest of all the 'minimum errors'

Decreasing the increment sizes of  $A_0$ ,  $\nu$  and  $\tau$  will increase the accuracy of the final estimates, but also increase the time required to try all parameter combinations. A graphical example of this method's results can be seen in Figure 6.

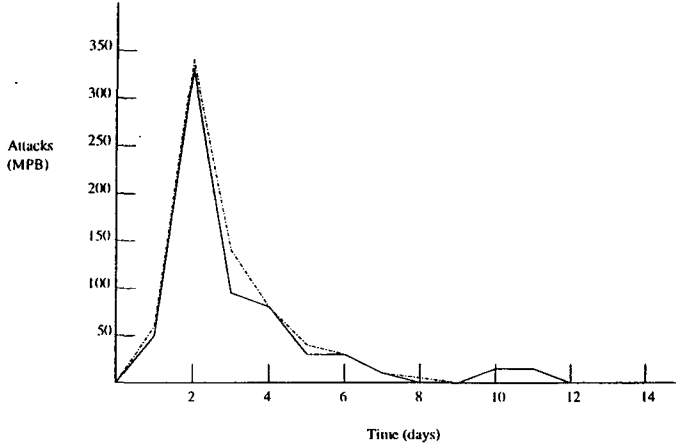


Figure 6: Comparison of manipulated experimental data ( $\{q_n, \ln(\frac{A_n r_0}{r_1 r_n})\}$ , solid line) and model predictions ( $\{q_n, \ln(I(q_n))\}$ , dashed line) of MPB attacks on an entire tree using the direct fitting procedure and the attack series of tree 1 from the 1995 SNRA data.

We applied this procedure to only a few attack series because of the large amount of computer time required. Data series which resulted in the best and worst fits using the indirect approach, including some which did not converge to real parameter values, were chosen. This enabled us to observe the differences and evaluate the merits of each technique, as well as determine the sensitivity of the estimates.

### 3 Results and Discussion

Of the twenty-seven trees in the 1995 SNRA plot, eight were successfully attacked and colonized by MPB. The indirect fitting method only converged on real parameters for MPB attack series of seven trees (Table 3). Estimated  $A_0$  values range from 3.8 to 13.4  $\mu\text{g}/\text{ha}$  with a weighted average towards the lower end at 6.7  $\mu\text{g}/\text{ha}$ . These values differ by about 10 units. Values of  $\nu$  show less variation, ranging from 2.5 to 7.0  $\text{ha}^2 \cdot \mu\text{g}^{-1} \cdot \text{fh}^{-1}$ . These still differ, however, by 4.5 units. The weighted average is 5.4  $\text{ha}^2 \cdot \mu\text{g}^{-1} \cdot \text{fh}^{-1}$ . Averages are weighted using corresponding  $r^2$  values. For  $A_0$  this is

$$\sum_{j=1}^{\text{all trees}} \left( \frac{r_j^2}{\sum_{i=1}^{\text{all trees}} r_i^2} (A_0)_j \right) \quad (12)$$

Using the direct method, estimates of  $A_0$  and  $\nu$  were obtained for all eight trees (Table 5). This method resulted in greater ranges in both parameter estimates, but consistently showed higher correlation coefficients.  $A_0$  ranges from 1.1 to 28.8  $\mu\text{g}/\text{ha}$  and has an average of 11.5  $\mu\text{g}/\text{ha}$ . The maximum and minimum differ by about 28 units, about three times the range associated with the indirect fitting method. Ranging from 0.3 to 9.2  $\text{ha}^2 \cdot \mu\text{g}^{-1} \cdot \text{fh}^{-1}$ ,  $\nu$  differs by almost 9 units. The weighted average is 3.5  $\text{ha}^2 \cdot \mu\text{g}^{-1} \cdot \text{fh}^{-1}$ .

In plot 1 of the 1996 St. Charles experiments, only the focus tree, out of forty total trees, was successfully colonized by MPB. That year plot 2 did little better with only eight out of thirty-five trees being colonized. Indirectly fitting the model to these trees' attack series resulted in estimates from only four of these trees (Table 3). Compared to 1995, this year's indirect estimates for  $A_0$  show less variability while estimates for  $\nu$  show more.  $A_0$  ranged from 2.9 to 6.2  $\mu\text{g}/\text{ha}$ , slightly over 3 units. The weighted average is 3.5  $\mu\text{g}/\text{ha}$ .  $\nu$  ranges over 12.5 units from 5.3 to 17.8  $\text{ha}^2 \cdot \mu\text{g}^{-1} \cdot \text{fh}^{-1}$ . The average 1996  $\nu$  value is 12.0  $\text{ha}^2 \cdot \mu\text{g}^{-1} \cdot \text{fh}^{-1}$ . Unlike the 1995 data, the direct method was not applied to all of the colonized trees from 1996, only those data sets which resulted in the best and worst indirect fits were used.

During the 1997 experiments, plot 1 near St. Charles had six trees, out of eighteen, colonized. Of sixteen host trees in plot 2, eleven were successfully colonized. The indirect fitting procedure converged upon parameter estimates for sixteen of the seventeen St. Charles trees (Table 4).  $A_0$  values range from 5.0 to 11.5  $\mu\text{g}/\text{ha}$ , a range of 6.5 units. The weighted average for these two plots is 8.4  $\mu\text{g}/\text{ha}$ , spanning 11 units from 0.6 to 11.9  $\text{ha}^2 \cdot \mu\text{g}^{-1} \cdot \text{fh}^{-1}$ ,  $\nu$  has an average of 3.7  $\text{ha}^2 \cdot \mu\text{g}^{-1} \cdot \text{fh}^{-1}$ .

The same year, SNRA plot 1 had only four of twenty-seven available hosts colonized. Plot 2 had a high percentage of trees colonized. Unfortunately, MPB activity in this plot began before we began making observations and the temporal structure of most attack series was lost. We were able to obtain indirect estimates of four trees' parameters. In plot 3, of thirty hosts, only five were successfully mass attacked and colonized. Of these five, one series resulted in indirect parameter estimates.

Considering the three 1997 SNRA plots together,  $A_0$  ranged from 1.9 to 12.9  $\mu\text{g}/\text{ha}$  with an average of 6.6  $\mu\text{g}/\text{ha}$ . Values of  $\nu$  span about 12 units from 1.7 to 13.9  $\text{ha}^2 \cdot \mu\text{g}^{-1} \cdot \text{fh}^{-1}$ . The weighted average is 5.0  $\text{ha}^2 \cdot \mu\text{g}^{-1} \cdot \text{fh}^{-1}$ .

The direct fitting method was applied to a few trees from the 1996 and 1997 experiments due primarily to the time investment required. The trees used and the plots in which they



**1995 and 1996 Indirect Parameter Estimates**

	Tree	$A_0$	$\nu$	$r^2$
SNRA 1995	1	3.8	7.0	0.95
	2	6.9	5.9	0.89
	3	4.7	6.0	0.05
	4	13.4	2.5	0.45
	5	6.2	5.1	0.72
	6	7.1	4.6	0.98
	7	5.5	6.2	0.33
Weighted Average		6.7	5.4	—
St. Charles 1996 Plot 1 Plot 2	1	3.4	8.8	0.76
	1	2.9	17.8	0.77
	2	2.5	13.9	0.94
	3	6.2	5.3	0.58
Weighted Average		3.5	12.0	—

Table 3: Estimates for  $A_0$  ( $\mu\text{g}/\text{ha}$ ) and  $\nu$  ( $\text{ha}^2 \cdot \mu\text{g}^{-1} \cdot \text{fh}^{-1}$ ) obtained by applying the indirect fitting method to the experimental data from 1995 and 1996 experiments. Averages are calculated using associated  $r^2$  values, according to (12).

are located are found in Table 5. Considering just the 1996 and 1997 results the direct method gave estimates of  $A_0$  ranging from 0.7 to 6.2  $\mu\text{g}/\text{ha}$ , the weighted average being 4.0  $\mu\text{g}/\text{ha}$ . Estimates for  $\nu$  show a bit more variation ranging from 1.3 to 18.6  $\text{ha}^2 \cdot \mu\text{g}^{-1} \cdot \text{fh}^{-1}$ . The weighted average for  $\nu$  is 6.5  $\text{ha}^2 \cdot \mu\text{g}^{-1} \cdot \text{fh}^{-1}$ .

Over all, estimates of  $A_0$  ranged from 2.5 to 13.4  $\mu\text{g}/\text{ha}$  from the indirect method (Table 6).  $A_0$  estimates show more variation using direct parametrization, 3.8 to 28.8  $\mu\text{g}/\text{ha}$ . The estimates for  $\nu$  show less variability, ranging from 0.6 to 17.8  $\text{ha}^2 \cdot \mu\text{g}^{-1} \cdot \text{fh}^{-1}$  when fitted indirectly and 1.1 to 9.2  $\text{ha}^2 \cdot \mu\text{g}^{-1} \cdot \text{fh}^{-1}$  when fitted directly.

The correlation coefficient of the indirect fits between predictions and data vary widely, spanning nearly the entire range of possible values. Tree 3 of the 1995 plot has an  $r^2$  value of 0.05, indicating a very poor fit, while tree 2 of 1997 SNRA plot 2 has an  $r^2 = 0.99$ , indicating a good fit. There is a considerably smaller spread in the indirect method's weighted averages;  $A_0$  ranging from 3.5 to 8.5  $\mu\text{g}/\text{ha}$  and  $\nu$  from 3.5 to 12.0  $\text{ha}^2 \cdot \mu\text{g}^{-1} \cdot \text{fh}^{-1}$ .

### 3.1 Parameter Estimate Variation

The variation in parameter estimates was not unexpected and there are several identifiable contributors. Some of the basic assumptions or generalizations used to construct the model do not hold true over time or space. The approximations of five flight hours per day, although an acceptable estimate, will naturally vary depending on individual plots physical location and daily temperature regimes. Another source of variation is found in the fact that we treat each tree and its associated chemotactic plume as if it were isolated from all other

### 1997 Indirect Parameter Estimates

	Tree	$A_0$	$\nu$	$r^2$
St. Charles 1997 Plot 1	1	5.8	5.7	0.95
	2	5.0	11.9	0.28
	3	5.0	2.8	0.62
	4	5.8	6.3	0.93
	5	10.3	3.4	0.97
	6	5.9	5.1	0.69
Plot 2	1	10.1	2.9	0.91
	2	9.2	0.6	0.12
	3	8.8	3.5	0.96
	4	8.9	3.7	0.45
	5	9.5	2.7	0.75
	6	11.5	3.0	0.97
	7	10.2	2.7	0.66
	8	9.2	2.9	0.53
	9	9.6	3.0	0.96
	10	7.7	1.7	0.95
Weighted Average		8.4	3.7	—
SNRA 1997 Plot 1	1	3.6	7.4	0.60
	2	5.8	5.6	0.21
	3	4.8	9.7	0.20
Plot 2	1	1.9	1.7	0.99
	2	9.1	3.4	0.90
	3	10.1	5.4	0.99
	4	4.3	13.9	0.20
Plot 3	1	12.9	4.7	0.31
Weighted Average		6.6	5.0	—

Table 4: Estimates for  $A_0$  ( $\mu\text{g}/\text{ha}$ ) and  $\nu$  ( $\text{ha}^2 \cdot \mu\text{g}^{-1} \cdot \text{fh}^{-1}$ ) obtained by applying the indirect fitting method to the experimental data from 1997 experiments. Averages are calculated using associated  $r^2$  values, according to (12).

**Direct and Indirect Parameter Estimates**

	Tree	Indirect			Direct		
		$A_0$	$\nu$	$r^2$	$A_0$	$\nu$	$r^2$
1995 SNRA	1	3.8	7.0	0.95	5.5	3.8	0.98
	2	6.9	5.9	0.89	28.8	1.3	0.96
	3	4.7	6.0	0.05	1.1	9.2	0.96
	4	13.4	2.5	0.45	15.0	1.1	0.78
	5	6.2	5.1	0.72	16.8	1.3	0.96
	6	7.1	4.6	0.98	8.8	5.7	0.99
	7	5.5	6.2	0.33	3.8	4.1	0.93
	8	**	**	***	13.2	0.3	0.79
1995 Weighted Average		6.7	5.4	—	11.5	3.5	—
1996 St. Charles	1 (plot 1)	3.4	8.8	0.76	4.2	18.6	0.98
	3 (plot 2)	6.2	5.3	0.58	5.1	6.7	0.97
	4 (plot 2)	**	**	***	0.7	8.8	0.97
1997 St. Charles SNRA	1 (plot 2)	10.1	2.9	0.91	4.4	3.3	0.96
	2 (plot 2)	9.2	0.6	0.12	5.9	1.7	0.85
	6 (plot 2)	11.5	3.0	0.97	5.8	3.1	0.99
	3 (plot 2)	10.1	5.4	0.99	4.7	3.1	0.99
	5 (plot 2)	**	**	***	0.9	7.7	0.99
	2 (plot 3)	**	**	***	6.2	1.3	0.36
1996-1997 Weighted Average		—	—	—	4.0	6.5	—

Table 5: Estimates for  $A_0$  ( $\mu\text{g}/\text{ha}$ ) and  $\nu$  ( $\text{ha}^2 \cdot \mu\text{g}^{-1} \cdot \text{fh}^{-1}$ ) obtained by applying the direct fitting method to the experimental data from certain trees' attack series. These are presented with corresponding estimates from the indirect method. Averages are calculated using associated  $r^2$  values, according to (12). The symbol \*\* indicates values for which the indirect fitting technique failed to converge.

**Summary of Parameter Estimates**

	Indirect			Direct		
	$A_0$	$\nu$	$r^2$	$A_0$	$\nu$	$r^2$
1995 Weighted Average	6.7	5.4	—	11.5	3.5	—
Combined Range	2.5-13.4	0.6-17.8	0.05-0.99	0.7-28.8	0.3-18.6	0.36-1.00
Combined Weighted Average	7.1	5.3	—	7.6	— 5.0	—

Table 6: Summary of estimates and ranges for  $A_0$  ( $\mu\text{g}/\text{ha}$ ) and  $\nu$  ( $\text{ha}^2 \cdot \mu\text{g}^{-1} \cdot \text{fh}^{-1}$ ) obtained by direct and indirect fitting techniques. The combined ranges and averages include all estimates, not simply yearly averages. Averages are calculated using associated  $r^2$  values, according to (12).

trees' plumes. In reality, there is certain to be some influence to the pheromone plume of one tree due to the pheromones emitted from MPB nesting in neighboring trees. This type of influence will vary from tree to tree depending on the spatial arrangement of a tree and its neighbors. This type of interaction is beyond the scope of this paper but is being addressed in another branch of the larger MPB project.

The scale at which the local model operates is also a likely source of variation in parameter estimates. When we approximate the average wind velocity as being linear and constant at 0.6 m/s, the model fails to account for the microclimate surrounding individual trees. Not only will wind conditions on both micro- and macro-scales vary from place to place and from moment to moment, but the temperature actually experienced on or just below the bark of a tree will also vary by aspect of the tree bole and relative position in the stand. The density of a particular stand of trees will have an impact on the microclimates surrounding individual trees. We fail to capture this variation when we treat all plots as having uniform tree density (by assigning  $\sigma = 0.5$ ) and use averages for temperature and wind velocity.

The effect of different size trees is also lost in the model because all trees are assumed to be of uniform size. This assumption will have an influence on  $A_0$  particularly. Trees of different sizes will have different carrying capacities of colonizing beetles [13]. This carrying capacity is, at some level, related to the point at which no new beetles are attracted to a tree, which in our model is described by  $A_0$ . Because the model assumes all trees to be uniform, this forces their carrying capacities to be equal as well. Consequently, when the model equations attempt to match true system dynamics, the value of  $A_0$  is not only trying to capture the chemical components of the system, but also the effects of the size of individual trees. In this sense,  $A_0$  is describing more of the system behavior than was intended, thus introducing a source of variation. To alleviate this problem a term accounting for individual tree size would be necessary.

The sources of variation in parameter estimation using the local model are not necessarily fatal problems. In the end we wish to obtain estimates to be used in the global model to describe system behavior in an entire forest, not to describe system behavior at a single spatial location. The use of averages (for wind speed or stand density, for example) make the estimated parameter values generally applicable and useful in the global model.

To evaluate the significance of the variation in the estimates of  $A_0$  and  $\nu$  we can consider the two non-dimensional combinations [23] in the infestation function, involving  $A_0$  and  $\nu$ .

$$\pi_1 = \frac{A_0 \nu}{\mu} \quad \text{and} \quad \pi_2 = \frac{a_1 q_{final}}{A_0 (4b_1 + w\delta_1)}$$

$\pi_1$  can be interpreted as the relative importance of pheromone-directed and random components of MPB behavior, while  $\pi_2$  measures the competitive ratio of pheromone contributions by MPB and environmental loss. With both  $A_0$  and  $\nu$  free to vary, the fitting procedures will actually be searching for values of  $\pi_1$  and  $\pi_2$  which result in the least sum of squares or smallest absolute error. Subsequently solving for the  $A_0$  and  $\nu$  results in their reported values. In the case of  $\pi_1$ , the individual values of  $A_0$  and  $\nu$  are less important than their product. Figure 7 shows points in  $\pi$ -space generated by indirect parameter estimates and MPB attack series on individual trees. Even though estimates vary widely from tree to tree, the fact that the points in  $\pi$ -space tend to cluster suggests that the model is capturing core

behavior but is failing to capture differences due to individual trees and the microclimates surrounding them.

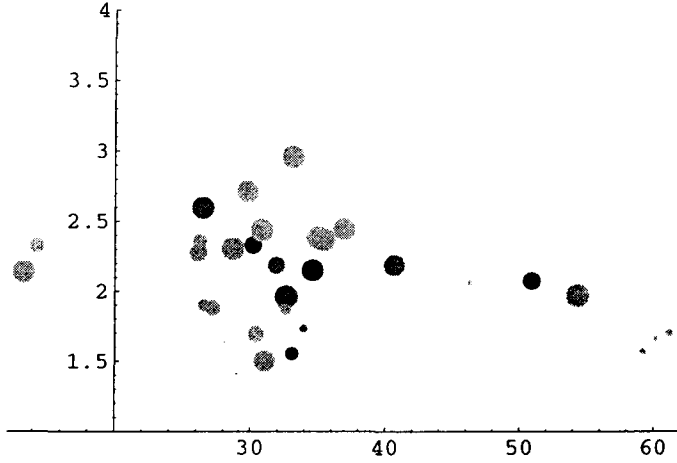


Figure 7: Points plotted in  $\pi$ -space. Each point is generated using the  $\pi_1$  and  $\pi_2$  values from a single tree, with the size scaled by the corresponding  $r^2$  value. Different shades represent different years' data; black circles represent 1996 data, dark grey represent 1995 data, and light grey represent 1997 data.

### 3.2 Comparison of Fitting Techniques

When comparing the indirect and direct fitting methods it is important to recall the intended purpose of each. The indirect method can be quickly applied to many data, sacrificing some degree of reliability. The direct method is more reliable in its estimates and may be used to determine the accuracy and overall effectiveness of the indirect method. This method, however, is much slower and more difficult to employ than the indirect method.

We use the indirect method primarily because it quickly and easily generates parameter estimates for many data sets. A weakness of this method is the many assumptions and simplifications required, which make estimated parameter values less reliable. Another problem is that the type of non-linear fitting technique used reveals nothing about the topology of the error surface upon which it is searching. It is therefore difficult to know whether estimates represent global or local minima. Additionally, separate calculations are required to determine the sensitivity of the model to particular parameters.

To determine the severity of the problems of the indirect method, we estimate parameter values by directly solving the model equations for systematic combinations of  $A_0$  and  $\nu$ . This requires fewer assumptions and provides error measurements for incremental values of parameters within a specified region, generating a picture of the error surface in parameter space. Figure 8 depicts the error surface for tree 6 from the 1995 SNRA data. This plot reveals a trend seen in all analyzed trees' error surfaces,  $A_0\nu = \text{constant} \sim \pi_1$ .

The direct method consistently produces a better fit between model predictions and observed data. The correlation coefficients are very high and for trees 3 and 5 from the 1997 SNRA plot 2, they round to 1.00. The weighted averages for the 1996 and 1997

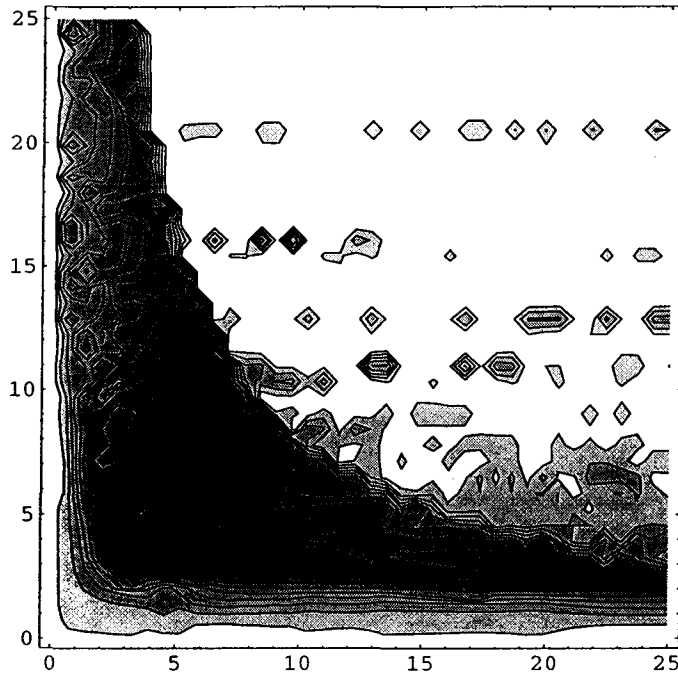


Figure 8: Error surface contours showing the measured error between model predictions and observational data for different values of  $A_0$  and  $\nu$  using data from tree 6 of the 1995 SNRA plot. Darker areas represent regions of smaller error.

trees are comparable to estimates obtained from the indirect method. This would suggest that despite its weaknesses, the indirect method is doing an acceptable job of estimating parameter values. The 1995 direct estimate of  $A_0$  agrees less with other estimates of  $A_0$ . It is considerably higher than expected. This is due to the the estimated value for tree 2. Removing this tree from the weighted average gives  $A_0 = 8.9 \mu\text{g}/\text{ha}$  and  $\nu = 3.5 \text{ ha}^2 \cdot \mu\text{g}^{-1} \cdot \text{fh}^{-1}$ , which agree much more closely with other years' estimates. Overall, the two methods appear to agree quite well in their estimates of the two parameters.

Parameter estimates for a tree obtained using the direct and indirect methods are different to a greater or lesser degree, but from the error surfaces generated by the direct method, we see that values obtained from the indirect method lie at local minimum of the surface. In some cases the local and true minima, even though they have different  $A_0$  and  $\nu$  values, have nearly the same associated error.

### 3.3 Validation

To truly test the validity of our best parameter estimates they should be tried on a global and not a local scale. Ultimately it is forest-sized dynamics we wish to predict. This type of analysis is currently underway and is showing promising results. As a cursory test of parameter estimates we compare their predictions on a local level.

To test how accurately the model predicts true system behavior using our best parameter estimates we compare its predictions with approximations of the final number of beetles nesting in a given tree. To approximate the final number of nesting beetles we counted

attacks within  $0.1225 \text{ m}^2$  at various heights on both the north and south aspects of colonized trees in both the St. Charles plots from 1997. We determined the density of attacks from the counted sections and multiplied by the total estimated area which was infested. Observed maximum attack heights ranged from 5.95 to 15.4 metres.

To produce model predictions the values  $A_0 = 7.6 \text{ } \mu\text{g/ha}$  and  $\nu = 5.0 \text{ ha}^2 \cdot \mu\text{g}^{-1} \cdot \text{fh}^{-1}$  were used. To determine the shape and magnitude of  $\gamma$  the procedure of the direct fitting technique was employed. Thus, this function varied from tree to tree. Individual trees' resin reservoirs,  $r_0$ , and rates at which resin is replenished,  $r_2$ , vary with tree size, so we approximate these parameters for each tree according to the relationships developed in [34]. Since resin is carried in the xylem layer of a tree the rest resin reservoir,  $r_0$ , is considered to be proportional to the ratio of xylem volume and the surface area of the tree. This ratio results in

$$r_0 \sim W \left( 1 - \frac{LR}{DBH} \right) LR$$

where  $W$  is the limiting growth factor,  $LR$  is the approximate depth of living wood (10.35 cm) and  $DBH$  is the diameter at breast height of the tree. We choose to normalize  $r_0$  so that a ten-inch DBH tree under no stress has  $r_0 = 1$ .

The rate of resin replenishment depends on the amount of "free energy" the tree has which can be directed towards resin production. In volumetric units this should be proportional to the ratio of new wood volume to the living wood volume. Thus, Powell *et al.* define a unitless tree "vigor",  $V$ , by

$$V \stackrel{def}{=} \frac{BAI}{\pi(DBH - LR)LR},$$

where  $BAI$  is a species-specific constant describing the basal area a tree can grow in one year. The resin replenishment rate of a tree will be proportional to the tree's vigor. Again, we normalize the  $r_2$  so that a 10 inch DBH lodgepole under no stress will have  $r_2/w = 0.1 \text{ fh}^{-1} \cdot R_0^{-1}$ .

Using the observed DBH from individual trees we calculated values for  $r_0$  and  $r_2$  with which to predict the final number of beetles nesting in a tree. From plot 1, the observed final numbers of nesting beetles are shown in Table 7. For trees 1 and 5 the model predicts fewer nesting beetles than observed. For the remaining four trees the model predicts larger numbers, always near 1300 MPB. Similar model predictions are seen for plot 2. The model consistently predicts more attacks than our field counts.

### 3.4 Biological Interpretation of Parameters

Our best estimate of  $\nu$  is  $5.0 \text{ ha}^2 \cdot \mu\text{g}^{-1} \cdot \text{fh}^{-1}$ . This parameter describes the strength of chemotactic attraction to the flying pheromones of nesting beetles. Its ecological significance is perhaps most easily understood through the role it plays in  $\pi_1$ . The numerator of this combination,  $A_0\nu$ , describes MPB movement as directed by chemical cues. The denominator,  $\mu$ , describes undirected beetle movement.  $\pi_1$  may be thought of as the ratio of the influence of chemical cues to the influence of randomness in beetle movement. A value of  $\pi_1 = 38$  means that beetle movement is directed about 38 times more strongly by pheromones than



1997 St. Charles Final Attacks			
	Tree	Observed	Predicted
Plot 1	1	1496	1369
	2	923	1293
	3	631	1373
	4	910	1322
	5	1391	1322
	6	567	1325
Plot 2	1	1300	1394
	2	1138	1389
	3	1076	1344
	4	722	1346
	5	863	1345
	6	704	1344
	7	728	1378
	8	791	1323
	9	693	1345
	10	987	1342
	11	760	1317

Table 7: Observed and predicted numbers of MPB nesting in colonized trees after the summer flight season has been completed. These trees are from the 1997 St. Charles plots. Predictions are made using the average parameter estimate and not specific estimates for each tree.

by pure randomness, which seems completely reasonable for an organism which must rely so heavily on spatial aggregation.

The parameter  $A_0$  is more difficult to interpret ecologically. For simplicity our model treats the MPB pheromone communication system as if it employs only one pheromone. We assume this chemical to be responsible for both the focusing and de-focusing of MPB attacks on a single tree dependent upon its local concentration. In these terms, the value  $A_0 = 7.6 \mu\text{g/ha}$  is easily interpreted. Below this concentration MPB attacks are focused upon the host tree, above this concentration MPB are discouraged from attacking. The true pheromone communication system involves multiple chemicals, each existing at its own concentration and exerting its own influence on flying MPB. Our estimate of  $A_0$  is not directly interpretable as the concentration of any one pheromone; instead, it represents the point in an attack series at which the cumulative pheromone effects switch from being focusing to de-focusing. Using the relationship between the global and local models, from (5), pheromone concentrations at a single location,  $A$ , can be written as a function of the number of nesting beetles,  $q$ , nesting in a tree in the following way

$$A = \frac{2a_1q}{4b_1 + w\delta_1}.$$

If  $A_0$  is the point at which pheromone effects switch from being focusing to de-focusing, by assigning it a value we can determine the number of beetles nesting in a tree when this switching occurs. Setting  $A \stackrel{\text{set}}{=} A_0 = 7.6$  gives

$$q_{\text{switch}} \doteq \frac{7.6(4b_1 + w\delta_1)}{2a_1} \approx 600 \text{ MPB}$$

## 4 Conclusion

In this paper we have used localization and two independent fitting procedures to estimate behavioral parameters for a spatially-extended, partial differential model for MPB dispersal and subsequent mass-attack on individual host pines. The major challenge we have overcome is in figuring out how to use point measurements (number of attacks on individual trees) to determine parameters ( $\nu, A_0$ ) which can only be understood in terms of their impact on spatially extended and averaged behaviors of densities of organisms. This was accomplished, and local validation measures used, to give some degree of confidence in our parameter predictions. In fact, considering the plethora of non-behavioral parameters which had to be estimated using scant literary and anecdotal evidence, the localized model did astonishingly well.

Of course, it would have been much more direct to have spatially extended measurements to parameterize the model, like those used by Turchin et. al. for southern pine beetle. We attempted these measurements for MPB and failed; we were unable to collect any reliable information on population density gradients in any of the three years of field observation. This underscores the importance of alternate strategies for parameterization.

There is a clear need for more work on parameterizing partial differential models of ecological systems. While there have been a wealth of models constructed, often with suggestive

or illuminating behavior, very little attention has been paid to problems associated with determining parameter values for these models. Without parameterization all of the suggestive modeling amounts only to consciousness-raising, and can not assist with practical questions in ecology.

It is those sorts of questions this work now frees us to address. The 'global' model for MPB dispersal can be used to investigate ideas relating to management and risk in this important forest ecosystem. Coupled with realistic models of forest and insect phenology the global dispersal model can be used to help understand factors contributing to epidemic outbreaks. Finally, given the current artificial nature of forest demographics, parameterized and validated spatial models will be required to envision and role-play scenarios for managing western forests back to a self-maintaining system in which MPB outbreak plays a healthy and self-limiting part.

## References

- [1] G.D. Amman and W.E. Cole. Mountain pine beetle dynamics in lodgepole pine forests. part II: population dynamics. *USDA Forest Service General Technical Report INT-145*, page 59, 1983.
- [2] B.J. Bentz. Unpublished data. Rocky Mountain Research Station, Logan Forestry Sciences Lab, Logan, Utah, 1995.
- [3] B.J. Bentz, J.A. Powell, and J.A. Logan. Localized spatial and temporal attack dynamics of the mountain pine beetle (*Dendroctonus ponderosae*) in lodgepole pine. *USDA/FS Research Paper INT-RP-494*, December 1996.
- [4] A.A. Berryman. Theoretical explanations of mountain pine beetle dynamics in lodgepole pine forests. *Env. Ent.*, 5(6):1225–1233, 1976.
- [5] A.A. Berryman. Towards a theory of insect epidemiology. *Res. Pop. Ecol.*, 19:181–96, 1978.
- [6] A.A. Berryman. Biological control, thresholds, and pest outbreaks. *Env. Ent.*, 11:544–49, 1982.
- [7] A.A. Berryman, K.F. Raffa, J.A. Millstein, and N.C. Stenseth. Interaction dynamics of bark beetle aggregation and conifer defense rates. *OIKOS*, 56:256–263, 1989.
- [8] A.A. Berryman, N.C. Stenseth, and D.J. Wollkind. Metastability of forest ecosystems infested by bark beetles. *Res. on Pop. Ecol.*, 26(1):13–29, 1984.
- [9] J.H. Borden, D.W.A. Hunt, D.R. Miller, and K.N. Slessor. Orientation in forest *Coleoptera*: an uncertain outcome of responses by individual beetles to variable stimuli. In T.L. Payne, M.C. Birch, and C.E.J. Kennedy, editors, *Mechanisms in Insect Olfaction*, pages 97–109. Oxford University Press, 1986.
- [10] J.H. Borden, L.C. Ryker, L.J. Chong, H.D. Pierce, B.D. Johnston, and A.C. Oehlschlager. Response of the mountain pine beetle, *Dendroctonus ponderosae*, to five semiochemicals in British Columbia lodgepole pine forests. *Can. J. For. Res.*, 17:118–128, 1987.
- [11] D.G. Burnell. A dispersal-aggregation model for mountain pine beetle in lodgepole pine stands. *Res. Popul. Ecol.*, 19:99–106, 1977.
- [12] W.E. Cole. The effects of intraspecific competition within mountain pine beetle broods under laboratory conditions. Res. note int-97, USDA Forest Service, 1962.
- [13] W.E. Cole and G.D. Amman. Mountain pine beetle infestations in relation to lodgepole pine diameters. Res. note int-95, USDA Forest Service, 1969.
- [14] J.E. Conn, J.H. Borden, B.E. Scott, L.M. Friskie, H.D. Pierce, and A.C. Oehlschlager. Semiochemicals for the mountain pine beetle, *Dendroctonus ponderosae*, in British Columbia: Field trapping studies. *Can J. For. Res.*, 13:320–324, 1983.
- [15] R.I. Gara and J.E. Coster. Studies on the attack behavior of the southern pine beetle III. Sequence of tree infestation within stands. *Contrib. Boyce Thompson Inst.*, 23:349–54, 1968.
- [16] D.R. Geiszler, V.F. Gallucci, and R.I. Gara. Modeling the dynamics of mountain pine beetle aggregation in a lodgepole pine stand. *Oecologia*, 46:244–253, 1980.

- [17] D.R. Geiszler and R.I. Gara. Mountain pine beetle attack dynamics in lodgepole pine. In A.A. Berryman, G.D. Amman, and R.W. Stark, editors, *Theory and practice of mountain pine beetle management in lodgepole pine forests: Symp. proc.* Wash. State Univ., Pullman, 1978.
- [18] P.R. Hughes. *Dendroctonus*: production of pheromones and related compounds in response to host monoterpenes. *Zeit. ang. Ent.*, 73:294–312, 1973.
- [19] D.W.A. Hunt, J.H. Borden, B.S. Lindgren, and G. Gries. The role of autoxidation of alpha-pinene in the production of pheromones of *Dendroctonus ponderosae*. *Can. J. For. Res.*, 19:1275–82, 1989.
- [20] W.H. Klein, K.L. Parker, and C.E. Jensen. Attack, emergence and stand depletion trends of the mountain pine beetle in a lodgepole pine stand during an outbreak. *Environ. Ent.*, 7:732–732, 1978.
- [21] L.M. Libbey, L.C. Ryker, and K.L. Yandell. Laboratory and field studies of volatiles released by *Dendroctonus ponderosae*. *Z. Angew. Entomol.*, 100:381–392, 1985.
- [22] J.A. Logan, P. White, B.J. Bentz, and J. Powell. Model analysis of spatial patterns in mountain pine beetle outbreaks. *Theoretical Population Biology*, 53:236–255, 1998.
- [23] J.D. Logan. *Applied Mathematics*. John Wiley and Sons, Inc., 1997.
- [24] Emily Martin, editor. *Mathematica 3.0: Standard Add-on Packages*. Copublishers: Wolfram Media and Cambridge University Press, 1996.
- [25] W.J. Mattson and N.D. Addy. Phytophagous insects as regulators of forest primary production. *Science*, 190:515–22, 1975.
- [26] W.F. McCambridge. Nature of induced attacks by the black hills beetle, *Dendroctonus ponderosae* (Coleoptera: Scolytidae). *Ann. Entomol. Soc. Am.*, 60:920–928, 1967.
- [27] H.A. Moeck and C.S. Simmons. Primary attraction of mountain pine beetle to bolts of lodgepole pine. *Can. Ent.*, 123:299–304, 1991.
- [28] T.E. Nebeker, J.D. Hodges, and C.A. Blanche. Host responses to bark beetle pathogen colonization. In T.D. Schowalter and G.M. Filip, editors, *Beetle-Pathogen Interactions in Conifer Forests*, pages 157–69. Academic Press, 1993.
- [29] G.B. Pitman. Trans-verbenol and alpha-pinene: their utility in manipulation of the mountain pine beetle. *J. Econ. Entomol.*, 64:426–430, 1971.
- [30] G.B. Pitman, J.P. Vite, G.W. Kinzer, and A.F. Fentiman. Bark beetle attractants: trans-verbenol isolated from *Dendroctonus*. *Nature*, 218:168–169, 1968.
- [31] A.D. Polymenopoulos and G. Long. Estimation and evaluation methods for population growth models with spatial diffusion: dynamics of mountain pine beetle. *Ecol. Modelling*, 51:97–121, 1990.
- [32] J. Powell, T. McMillen, and P. White. Connecting a chemotactic model for mass attack to a rapid integro-difference emulation strategy. *SIAM J. Appl. Math.*, 1997. In press.
- [33] J. Powell, P. White, T. McMillen, Z. Biesinger, B. Kennedy, J. Tams, B. Bentz, J. Logan, and D. Roberts. State and implementation of the mountain pine beetle dispersal model. Technical report, Department of Mathematics and Statistics, Utah State University, Logan, Utah 94322-3900, 1997.

- [34] J.A. Powell, B. Kennedy, P. White, B. Bentz, J. Logan, and D. Roberts. Mathematical elements of attack risk analysis for mountain pine beetle. *Unpublished Data*, 1998.
- [35] J.A. Powell, J.A. Logan, and B.J. Bentz. Local projections for a global model of mountain pine beetle attacks. *J. Theor. Biol.*, 179:243–60, 1996.
- [36] J.A. Powell and J.D. Rose. Local consequences of a global model for mountain pine beetle mass attack. *Dynamics and Stability of Systems*, 12:3–24, 1997.
- [37] J.A. Powell, J. Tams, B.J. Bentz, and J.A. Logan. Theoretical analysis of ‘switching’ in a localized model for mountain pine beetle mass attack. *J. Theor. Biol.*, 194:49–63, 1997.
- [38] H.K. Preisler and K. Haiganoush. Colonization patterns of the mountain pine beetle in thinned and unthinned lodgepole pine stands. *Forest Science*, 39:528–45, 1993.
- [39] K.F. Raffa and A. A. Berryman. The role of host plant resistance in the colonization behavior and ecology of bark beetles (*Coleoptera: Scolytidae*). *Ecol. Monogr.*, 53:27–49, 1983.
- [40] K.F. Raffa and A. A. Berryman. A mechanistic computer model of mountain pine beetle populations interacting with lodgepole pine stands and its implications for forest managers. *Forest Sci.*, 32(3):789–805, 1986.
- [41] K.F. Raffa and A.A. Berryman. Flight responses and host selection by bark beetles, pp. In A.A. Berryman and L. Safranyik, editors, *Dispersal of Forest Insects: Evaluation, Theory and Management Implications*, pages 213–233. Washington State University, Pullman, Washington, 1979.
- [42] K.F. Raffa, T.W. Phillips, and S. M. Salom. Strategies and mechanisms of host colonization by bark beetles. In T.D. Schowalter and G.M. Filip, editors, *Beetle-Pathogen Interactions in Conifer Forests*, pages 103–120. Academic Press, N.Y., 1993.
- [43] R.W. Reid. Biology of the mountain pine beetle, *Dendroctonus monticolae*, in the East Kootenay region of British Columbia III. Interaction between the beetle and its host, with emphasis on brood mortality and survival. *Can. Ent.*, 95:225–238, 1963.
- [44] R.W. Reid, H.S. Whitney, and J.A. Watson. Reactions of lodgepole pine to attack by *Dendroctonus ponderosae* hopkins and blue stain fungi. *Can. J. Botany*, 45:1115–6, 1967.
- [45] J.A.A. Renwick and J.P. Vite. Systems of chemical communication in *Dendroctonus*. *Contributions of the Boyce Thompson Institute*, 23:355–360, 1970.
- [46] D.W. Roberts. A dynamical systems perspective on vegetation theory. *Vegetation*, 69:27–33, 1987.
- [47] A.L. Roe and G.D. Amman. The mountain pine beetle in lodgepole pine forests. *USDA For. Serv. Res. Pap.*, INT-71, 1970.
- [48] W.H. Romme, D.H. Knight, and J.B. Yavitt. Mountain pine beetle outbreaks in the Rocky Mountains: regulators of primary productivity? *Am. Nat.*, 127:484–94, 1986.
- [49] J.A. Rudinsky, M.E. Morgan, L.M. Libbey, and T.B. Putnam. Antiaggregative-rivalry pheromone of the mountain pine beetle, and a new arrestant of the southern pine beetle. *Environ. Entomol.*, 3:90–98, 1974.

- [50] L.C. Ryker and K.L. Yandell. Effect of verbonone on aggregation of *Dendroctonus ponderosae* Hopkins (*Coleoptera: Scolytidae*) to synthetic attractant. *Entomol.*, 96:452–459, 1983.
- [51] L. Safranyik, R. Silversides, L.H. McMullen, and D.A. Linton. An empirical approach to modeling the local dispersal of the mountain pine beetle (*Dendroctonus ponderosae* Hopkins) in relation to sources of attraction, wind direction and speed. *J. Appl. Ent.*, 108:498–511, 1989.
- [52] T.D. Schowalter, R.N. Coulson, and D.A. Crossley. Role of southern pine beetle and fire in maintenance of structure and function of the southeastern coniferous forest. *Env. Ent.*, 10:821–825, 1981.
- [53] R.H. Smith. Toxicity of pine resin vapors to three species of *Dendroctonus* bark beetles. *J. Econ. Ent.*, 56:827–31, 1963.
- [54] R.H. Smith. Resin quality as a factor in the resistance of pines to bark beetles. In H.D. England, R.E. Gerhold, R.E. McDermot, E.J. Schreiner, and J.A. Winieski, editors, *Proceedings of the NATO and National Science Foundation*, pages 189–96. Pergamon Press, Oxford, England, 1966.
- [55] H. Tennekes and J.L. Lumley. *A First Course in Turbulence*. MIT Press, 1975.
- [56] P. Turchin. Population consequences of aggregative movement. *J. Anim. Ecol.*, 58:75–100, 1989.
- [57] P. Turchin and W.T. Thoeny. Quantifying dispersal of southern pine beetles with mark-recapture experiments and a diffusion model. *Ecol. Appl.*, 3:187–198, 1993.
- [58] D.L. Wood. Selection and colonization of ponderosa pine by bark beetles. *Symp. Royal Entomolog. Soc. London*, 6:110–117, 1972.



# A Appendix 1 – Estimating ‘Local’ Parameter Values

## A.1 Chemical Diffusion Parameters

In an early version of the model [35] the flux due to beetles’ attraction to and inhibition to the suite of pheromones,  $A$ , was modeled as

$$\Phi = \nu P(A_0 - A)\nabla A,$$

where  $P$  is the population of flying beetles [35, 36]. This model did not work well for large values of  $A$ . It had the effect of not only inhibiting beetle attacks on a tree, but also reduced all attacks in the area. To better fit empirical evidence,  $A_3$ , a parameter describing the maximum saturation concentration of pheromones, was added. This has the effect that, once pheromone concentrations reach a certain value, higher concentrations will not further inhibit beetle attacks. The new model for chemotaxis is

$$\Phi = \nu P \frac{A_0 - A}{A_0 + A/A_3} \nabla A.$$

This flux function has the effect of attracting beetles for small  $A$  and inhibiting beetles for large  $A$ , parametrized by  $A_3$  for  $A > A_0$ . We have chosen a value for  $A_3$  that, for small  $A$ , will behave much like the earlier model and still allow the saturating effect to restrain the inhibition as  $A$  grows large. A value of  $A_3 = 1$  was chosen, which has the effect that as  $A$  gets large the flux is approximately

$$\Phi = -\nu P \nabla A, \tag{13}$$

and as  $A$  gets small the flux is approximately

$$\Phi = \nu P \nabla A, \tag{14}$$

so that neither peak inhibition nor attraction depend directly on the magnitude of  $A$ , but only on its gradient. This is reasonable since beetles respond to chemical gradients, not necessarily absolute amounts.

To estimate the rate of pheromone production,  $a_1$ , we refer to Borden *et al.* [9]. They estimate the production rate of *trans*-verbenol by a female MPB at about 20 ng/fh, giving

$$a_1 = 2 \mu\text{g} \cdot \text{fh}^{-1} \cdot \text{HMPB}^{-1}.$$

The parameters  $b_1$  and  $\delta_1$ , the rate of pheromone diffusion and the loss rate of pheromone, respectively, can be estimated simultaneously. The self-modifying spatial behavior of the system is mediated by the pheromone plume produced by nesting MPB. One model for the diffusion of the pheromone plume produced by  $q$  nesting MPB at the origin would be

$$A_t - uA_x = b_1 A_{yy} + b_2 A_{xx} - \delta_1 A + a_1 q \delta(x, y),$$

where  $u$  is the average wind speed, which we will assume is directed along the  $x$  axis in the positive direction. We also assume, based on observations of smoke plumes, that the diffusion in the direction of the wind itself is small ( $b_2 \simeq 0$ ). Taking  $a_1$  to be  $2 \mu\text{g} \cdot \text{fh}^{-1} \cdot \text{HMPB}^{-1}$ , to determine the remaining parameters,  $b_1$  and  $\delta_1$  we rely on dimensional arguments. As in [55], let  $\xi$  be the average separation between hosts ( $\sim 3$  metres) in an open-canopy stand. We estimate the scale of losses to satisfy

$$\xi^2 \simeq \frac{b_1}{\delta_1},$$

so that characteristic losses occur on a tree-to-tree scale in open-stand conditions. The rate of chemical mixing due to turbulence we relate to the advection generated by solution via method of steepest descents. Solving these two expressions for  $b_1$  and  $\delta_1$  gives

$$b_1 = \frac{u\xi}{2} \quad \text{and} \quad \delta_1 = \frac{u}{2\xi}.$$

As the canopy of a stand becomes more closed the air below the canopy becomes more isolated from the air above. While for a particular choice of  $u$  this should not change the rate of horizontal diffusion, it will influence the rate of loss through the canopy. We therefore augment the descriptions of  $b_1$  and  $\delta_1$  with a scaling factor,  $\sigma$ , reflecting the degree of closure of the canopy ( $\sigma = 1$  indicates open stand conditions,  $\sigma = 0$  indicates a solid canopy). Choosing an average wind speed of  $u = 0.6$  m/s and an average spatial scale of loss of  $\xi = 3$  m gives  $b_1 = \frac{0.324}{\sigma}$  ha/fh and  $\delta_1 = 360\sigma$  fh<sup>-1</sup>. We use an average value of  $\sigma = 0.5$ . From an informal sensitivity analysis, variations in  $\sigma$  have only a small effect on parameter estimates.

## A.2 Resin Response Parameters

The parameter  $r_0$  describes the constitutive resin reservoir of a lodgepole of 10 inch diameter at breast height under no environmental stress, and can be related to the volume of resin in a tree. We can non-dimensionalize this parameter by scaling all measures of resin capacity to the health of a vigorous, unstressed tree, setting the value to 1 for a 10 inch lodgepole, which is approximately the average size we dealt with. To simplify unit analysis this can be denoted by units of  $[wR_0]$ , where  $R_0$ , a global parameter, describes volume of resin per area, so that

$$r_0 = w R_0 = 1.$$

The size of a tree being attacked is described by  $w$ . It is important to note that this is not the basal area or crown area of a tree, but more a description of the area in which a tree is the dominant feature. A reasonable estimate of this is 3 m<sup>2</sup> cross-sectional area. In hectares this is

$$w = 0.003 \text{ ha}.$$

To estimate the mortality rate of MPB due to host defenses,  $\beta$ , the rate of resin replenishment and outflow through attack holes,  $r_2$  and  $r_3$ , respectively, and the rate of resin crystallization,  $r_4$ , we write and solve a system of equations involving these four parameters.

The first system equation is written assuming that a general attack rate of 5 HMPB over a 5-day period is just barely sufficient for overwhelming a healthy tree's defenses [5, 58]. Estimating there to be 5 flight hours (fh) in a day, this translates into an infestation rate of 0.20 HMPB per flight hour. Using this in (6) in place of the infestation term should correspond to  $\dot{q} = 0$  giving

$$0.2 \frac{\text{HMPB}}{\text{fh}} = 0.2 \frac{\text{HMPB}}{\text{fh}} - \beta \frac{r_3}{w} q r. \quad (15)$$

At this point the tree should be able to replenish its resin reserves at the same rate as they are being depleted by attacking beetles, thus no net change should be seen. From the steady state of (8) we have  $r = r_0 - \frac{r_3}{r_2} h$ . Assuming the number of attack holes to be approximately equal to the number of attacking female beetles and replacing  $r$  in (15) results in

$$0.2 \frac{\text{HMPB}}{\text{fh}} = \beta \frac{r_3}{w} r_0 q \left( 1 - \frac{r_3}{r_0 r_2} q \right). \quad (16)$$

In this form, the resin capacity of a tree is a function of numbers of nesting beetles,  $f(q) = q \left(1 - \frac{r_3}{r_0 r_2} q\right)$ . This quadratic has zeros at  $q = 0$  and  $q = r_0 r_2 / r_3$ , and has the form of a parabola with its maximum midway between the zeros, meaning that the maximum response of the tree will be when  $q = r_0 r_2 / 2 r_3$ . Using this value in (16) we have

$$0.2 \frac{\text{HMPB}}{\text{fh}} = \frac{\beta r_2}{4w}$$

where  $r_0$  has been replaced with its value of 1. Unit analysis reveals the units of  $\beta$  to be  $\text{ha}^{-1} \cdot R_0^{-1}$ .

Since global model variables describe densities rather than numbers at a point, the parameters  $r_2$  and  $r_3$  must also describe rates involving densities. To use them in the local model they must be converted to rates involving numbers. This can be accomplished by dividing by  $w$ , the characteristic size of a tree. To avoid introducing new parameters we use the ratios  $r_2/w$  and  $r_3/w$ . Assuming a tree to be under no stress,  $r_2$  should be approximately equal to  $r_3 r_4$ , meaning that the rate at which a tree can replenish its resin reserves should be about equal to the rate at which it flows out and crystallizes. That is

$$r_2 = r_3 r_4.$$

The third system equation is obtained by considering equation (8). This has steady states at  $r = 0$  and  $r = r_0 - \frac{r_3}{r_2} h$ . The solution of interest is

$$r = r_0 - \frac{r_3}{r_2} h.$$

Observing that there should be a value for  $h$  which is sufficient to deplete the constitutive resin capacity of the tree, we estimate this value to be about 2 HMPB [12, 43, 41, 20]. So, when  $r = 0$ ,  $h = 2$ , with  $r_0 = 1$ , we have

$$\frac{r_3}{r_2} = 0.5 \text{ ha} \cdot R_0.$$

For the final equation we estimate that it requires one to two days (5 to 10 fh) for resin to crystallize. Recalling (7) and taking there to be no continued infestation of an initially attacked, healthy tree ( $r = r_0 = 1$ ), we have

$$\dot{h} = -\frac{r_3}{w} r_4 h.$$

The solution to this differential equation is ( $h$  is dependent upon time)

$$h = h_0 \exp\left(-\frac{r_3}{w} r_4 \Delta t\right).$$

Assuming that after two days the number of holes left unfilled by resin should be nearly zero, we can say that this should be approximately equal to  $h = h_0 \exp(-1)$ . Comparing these two equations gives the relationship,

$$1 = 10 \frac{r_3}{w} r_4,$$

which results in an estimate of

$$\frac{r_3}{w} r_4 = 0.1 \text{ ha}^{-1} \cdot \text{fh}^{-1} \cdot R_0^{-1}.$$

This equation completes our system involving  $\beta$ ,  $r_2$ ,  $r_3$ , and  $r_4$  :

$$\begin{aligned} 0.2 &= \frac{\beta r_2}{4w}, \\ r_2 &= r_3 r_4, \\ \frac{r_3}{r_2} &= 0.5, \\ \frac{r_3}{w} r_4 &= 0.1. \end{aligned}$$

Solving this system we estimate

$$\begin{aligned} \beta &= 8 \text{ ha}^{-1} \cdot R_0^{-1}, \\ \frac{r_2}{w} &= 0.1 \text{ ha}^{-1} \cdot \text{fh}^{-1} \cdot R_0^{-1}, \\ \frac{r_3}{w} &= 0.05 \text{ fh}^{-1}, \\ r_4 &= 2 \text{ ha}^{-1} \cdot R_0^{-1}. \end{aligned}$$

### A.3 MPB Response Parameters

To estimate the diffusivity of flying beetles due to random redistribution we refer to experiments of Turchin and Theony [57]. They estimate a parameter for the southern pine beetle,  $B$ , which is related to the ratio of diffusion rate ( $\mu$ ) and loss rate of the population ( $r_1 + \omega_1$ ) in the following way:

$$B \equiv \sqrt{\frac{D}{\delta}} = \sqrt{\frac{\mu}{r_1 + w_1}}$$

where  $D$ , is their diffusion rate, and  $\delta$ , their rate at which beetles are lost from the dispersing population.

Their estimates of  $B$  range from 0.19 to 4.8  $\text{ha}^{-1}$ . Taking  $B = 2.4 \text{ ha}^{-1}$  and our values of  $\omega_1 = 0.014 \text{ fh}^{-1}$  and  $r_1 = 0.16 \text{ fh}^{-1}$  we can solve for  $\mu$ :

$$\mu = 1.0 \text{ ha/fh}.$$

To estimate the rate at which flying MPB land due to randomness only and not in response to chemical cues, we assume that 15% of the flying beetles will randomly land and attack trees per flight hour. At any time,  $t$ , the population of flying beetles can be written

$$P_t = -r_1 P.$$

The solution to this is

$$P = P_0 e^{-r_1 t}.$$

At time  $t = 1 \text{ fh}$  the population should only have decreased by 15%, leaving 85% of the original population. Substituting these in the solution gives

$$0.85 P_0 = P_0 e^{-r_1}.$$

Solving for  $r_1$  gives

$$\begin{aligned} r_1 &= -\ln(0.85) \text{ fh}^{-1} \\ &= 0.16 \text{ fh}^{-1}. \end{aligned}$$

We estimate the maximum distance away from a tree a flying beetle can be and still be visually attracted to it as  $r_e = 2$  metres. This acts as a conversion factor for transforming the density of flying MPB into the number of MPB attacking a tree. In units of hectares

$$r_e = 0.02 \text{ ha}^{\frac{1}{2}}.$$

This research was supported in part  
by funds provided by the  
Rocky Mountain Research Station,  
Forest Service  
U. S. Department of Agriculture